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Coastal upwelling affects filter-feeder stable isotope composition across three continents

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ABSTRACT

Large-scale nutrient fertilisation by coastal upwelling promotes benthic productivity through energy subsidies from enhanced phytoplankton production, and predictions of alterations to upwelling under climate change have implications for benthic ecosystem functioning. We investigated the stable isotope compositions of two bioengineers of global significance, the mussels *Perna perna* and *Mytilus galloprovincialis*, from upwelling and non-upwelling sites in five upwelling systems. Samples from Brazil, South Africa and Oman exhibited lower $\delta^{13}C$ values at upwelling sites than at non-upwelling sites, with clearer effects where upwelling is more intense and frequent. North West Africa showed variability, probably linked to Saharan dust input. We highlight the importance of upwelling to sustaining benthic primary consumers and the sensitivity of consumer diet to the intensity and frequency of upwelling within each region. These results have implications in relation to climate change scenario effects on upwelling events, with potential cascading effects on higher trophic levels and ecosystem functioning.

1. Introduction

The last glacial period was characterized by the existence of spatial refugia that allowed species to persist in the face of global cooling (Dobrowski, 2011; Lourenço et al., 2016). We now face dramatic environmental changes through global warming and it has recently been shown that coastal upwelling cells, where cold, nutrient rich deep water comes to the surface, can act as potential refugia from increasing temperatures for intertidal species (Lourenço et al., 2016). Coastal upwelling occurs across the globe, and alterations to upwelling regimes will have important consequences in terms of the temperatures to which marine species are exposed (Gaylord and Gaines, 2000). Even more directly, because upwelling entails the broad-scale fertilisation of the water column and alterations to upwelling regimes will affect food availability along enormous stretches of coastline (Puccinelli et al., 2016a; Docmac et al., 2017).

The regulation of primary production in the ocean is complicated by the fact that new nutrient availability and usage are usually spatially separated. New nutrient production largely occurs in deep waters, below the depths to which light penetrates, while photosynthesis is restricted to the surface euphotic zone (Clark et al., 2016). As a result, the advection of cold, nutrient-rich deep waters to the surface by upwelling is a crucial link between new nutrient production and usage. Coastal upwelling thus has a key influence on primary and secondary production by fertilizing coastal habitats, driving phytoplankton blooms (Tilstone et al., 2000), sustaining benthic populations at high densities (Smith et al., 2009) and representing a key factor responsible for supporting many of the world's most productive fisheries (Ward et al., 2006).

Marine systems are strongly shaped by physical processes and the ocean is responding to climate change not only through warming and acidification (Genner et al., 2004; Hoegh-Guldberg et al., 2007), but also through increasing wind stress (Narayan et al., 2010). Wind stress affects primary production through its influence on water column stratification and on the intensity and frequency of upwelling events (Doney et al., 2012), and there is long-term evidence that upwelling frequency is increasing in several parts of the globe (Sydeman et al., 2014). Alterations to upwelling modify the composition of the phytoplankton community and thus the quantity and quality of the food available for primary consumers, with direct and indirect effects on

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their metabolism and fitness, which can then affect energy flux to higher trophic levels (Frederiksen et al., 2006).

We aimed to evaluate the degree of dependence of costal systems on upwelling by determining whether primary consumers exhibit a discernible influence of upwelling effects on phytoplankton production, using stable isotope (SI) analysis. Phytoplankton and macroalgae are the main primary producers in coastal systems and exhibit marked differences in their isotopic compositions and this results in a marked onshore/offshore gradient in the SI composition of suspended particulate material (SPM) in the water column (Hill et al., 2008; Mallela and Harrod, 2008). We hypothesised that changes in the average relative abundances of different materials in SPM should be reflected in the isotopic composition of filter-feeders, with different values where diets are more or less heavily dominated by phytoplankton, and that discernible reductions in $\delta^{13}C$ values would be observed at sites influenced by upwelling. This was supported by a preliminary study of mussels and barnacles on the coast of South Africa (Puccinelli et al., 2016a), with significant lower $\delta^{13}C$ values at upwelling sites, highlighting the increased importance of phytoplankton in their diet (Puccinelli et al., 2016c, a). This has direct implications for how coastal populations are likely to respond to ongoing alterations to global patterns of wind stress and upwelling intensity.

Here, we tested the generality of upwelling effects by examining the isotope composition of two filter-feeder species of global significance from recognised upwelling and non-upwelling regions within five very different systems in the Indian and Atlantic Oceans. Because isotope fractionation can differ among species and even among tissues, we restricted our study to two widespread species, the brown mussel *Perna perna* and the blue mussel *Mytilus galloprovincialis*, comparing three different tissues within each individual, as tissues exhibit different turnover rates and thus integrate a dietary signal over different time periods.

2. Material and methods

2.1. Study areas

The intertidal rocky shores of Morocco and Western Sahara (referred to collectively as North West Africa), South Africa, Brazil and Oman were investigated (Fig. 1). All these countries include areas that are characterized by wind driven upwelling events, occurring primarily during spring/summer, and that are spatially interspersed with non-upwelling areas.

In South Africa, upwelling occurs predominantly along the south and west coasts, which are classified as separate biogeographic provinces (Emanuel et al., 1992). The eutrophic west coast Benguela System experiences strong, wind-driven upwelling events in austral spring and summer (Andrews and Hutchings, 1980). In contrast, the south coast is dominated by the oligotrophic Agulhas System, with a semi-permanent upwelling cell located close to Port Alfred in the south-east side of the coast. Elsewhere on this coast the frequency and intensity of upwelling are variable (Lutjeharms et al., 2000). To separate the effects of biogeography and upwelling, we considered the two coasts as separate systems.

The Atlantic coast of North West Africa is influenced by the Canary Current, a southward flowing current that receives oligotrophic water from the subtropical North Atlantic Gyre and upwelled water from the North Atlantic Central Water (Hagen, 2001). Upwelling in this region occurs over the shelf and shelf-break during summer and early autumn (Hagen, 2001). Additionally, this region is characterized by topographically-driven filaments of water located off Cape Ghir, which transport upwelled water offshore throughout the year (Van Camp et al., 1991). This coast also receives nutrient input, including iron and phosphate, from Saharan dust (Pabortsava et al., 2017).

The southern part of the Omani coast is influenced by the fast-flowing Somali Current, which changes direction with the monsoon season (Currie, 1992; Al-Hashmi et al., 2010). During boreal summer, the warm Southwest monsoon moves coastal waters north-eastward, creating coastal wind-driven upwelling between June and October (Piontkovski and Al-Jufaili, 2013). The Northeast monsoon reverses the pattern during the rest of the year (Shi et al., 2000).

The coast of Brazil is influenced by the warm oligotrophic waters of the subtropical Brazil Current which originates from the South Atlantic Subtropical Gyre. The current flows southwards between 19 and 31°S along the 200 m isobath, which represents the continental break (Campos et al., 2000). The region experiences shelf break upwelling driven by the Brazil Current cyclonic meander, predominantly during September–April, with upwelling events more pronounced in the Cabo Frio region (Sites 1B, 2B, 3B; Gonzalez-Rodriguez et al., 1992).

2.2. Sampling sites

Samples were collected at intertidal rocky shore sites representing both recognised upwelling areas and sites with little/no influence of upwelling. Sites were chosen based on published literature in which in situ and satellite chlorophyll *a* and temperature data were used to define upwelling and non-upwelling areas (Lutjeharms et al., 2000; Xavier et al., 2007; Cole and McQuaid, 2010; Piontkovski and Al-Jufaili, 2013; Lourenço et al., 2016; Puccinelli et al., 2016c). Sites representing the two conditions were geographically interspersed where possible within relatively narrow latitudinal regions to avoid latitude effects (Rau et al., 1982), with equal numbers of sites per condition in each region except

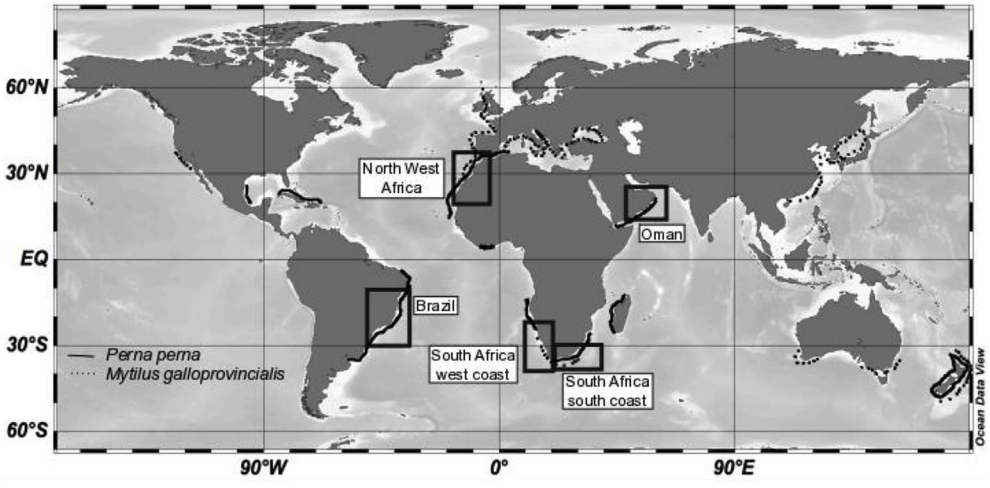

Fig. 1. Map showing the distribution of the target species of this investigation, *Perna perna* (solid line) and *Mytilus galloprovincialis* (dotted line), and the five sampling regions where samples of mussels were collected: South Africa west coast, South Africa south coast, North West Africa, Oman and Brazil. Samples were collected at upwelling and non-upwelling sites in each region.

Table 1
Table indicating information on sampling sites, time of collection and preservation method of two mussel species (*Perna perna* and *Mytilus galloprovincialis*) collected at upwelling and non-upwelling sites from five upwelling regions: South Africa south and west coast, North West Africa, Brazil and Oman.

Region	Time	Species	Preservation	Upwelling	Site Code	Site Name	Latitude	Longitude
South Africa-west coast	2013	*M. galloprovincialis*	Liquid nitrogen	upwelling	1W	Groenrivier	−34.005	18.341
	2012/2013			non-upwelling	2W	Doring Bay	−33.806	18.463
	2012/2013			upwelling	3W	Elandsbaai	−32.807	17.883
	2013			non-upwelling	4W	Paternoster	−32.317	18.321
	2012			non-upwelling	5W	Bloubergstrand	−31.816	18.232
	2012			upwelling	6W	Llandudno	−30.852	17.575
South Africa- south coast	2012/2013	*P. perna*	Liquid nitrogen	non-upwelling	1S	Kidd's Beach	−33.152	27.701
	2012/2013			upwelling	2S	Port Alfred	−33.482	27.152
	2012/2013			non-upwelling	3S	Jeffreys Bay	−34.049	24.927
	2013			upwelling	4S	Cape St Francis	−34.211	24.829
	2012			upwelling	5S	Knysna	−34.084	23.043
North West Africa	2013	*P. perna & M. galloprovincialis*	70% ethanol	non-upwelling	1M	Lorache	35.193	−6.162
				non-upwelling	2M	Rabat	33.978	−6.905
				upwelling	3M	Essaouira	31.514	−9.773
				upwelling	4M	Imsouane	30.847	−9.823
				non-upwelling	5M	Tan Tan	28.648	−11.162
				non-upwelling	6M	Tarfaya	27.924	−12.953
				upwelling	7M	Boujdour	26.117	−14.495
				upwelling	8M	Qued Kraa	25.838	−14.576
Oman	2014	*P. perna*	−20 °C freezer	non-upwelling	1O	Al Khabbah	22.229	59.809
	2016		70% ethanol	non-upwelling	2O	Duqm	19.524	57.698
	2016		70% ethanol	upwelling	3O	Ras Madrakan	18.978	57.809
	2016		70% ethanol	upwelling	4O	Hasik	17.448	55.259
	2014		−20 °C freezer	upwelling	5O	Mirbat	16.999	54.688
Brazil	2015	*P. perna*	−20 °C freezer	upwelling	1B	Prainha	−22.977	−42.035
				upwelling	2B	Atalaia	−22.986	−42.009
				upwelling	3B	Ponta da Cabeca	−22.954	−42.024
				non-upwelling	4B	Sao Pedro	−23.872	−46.137
				non-upwelling	5B	Praia Branca	−23.874	−46.139
				non-upwelling	6B	Praia Preta	−23.907	−46.159

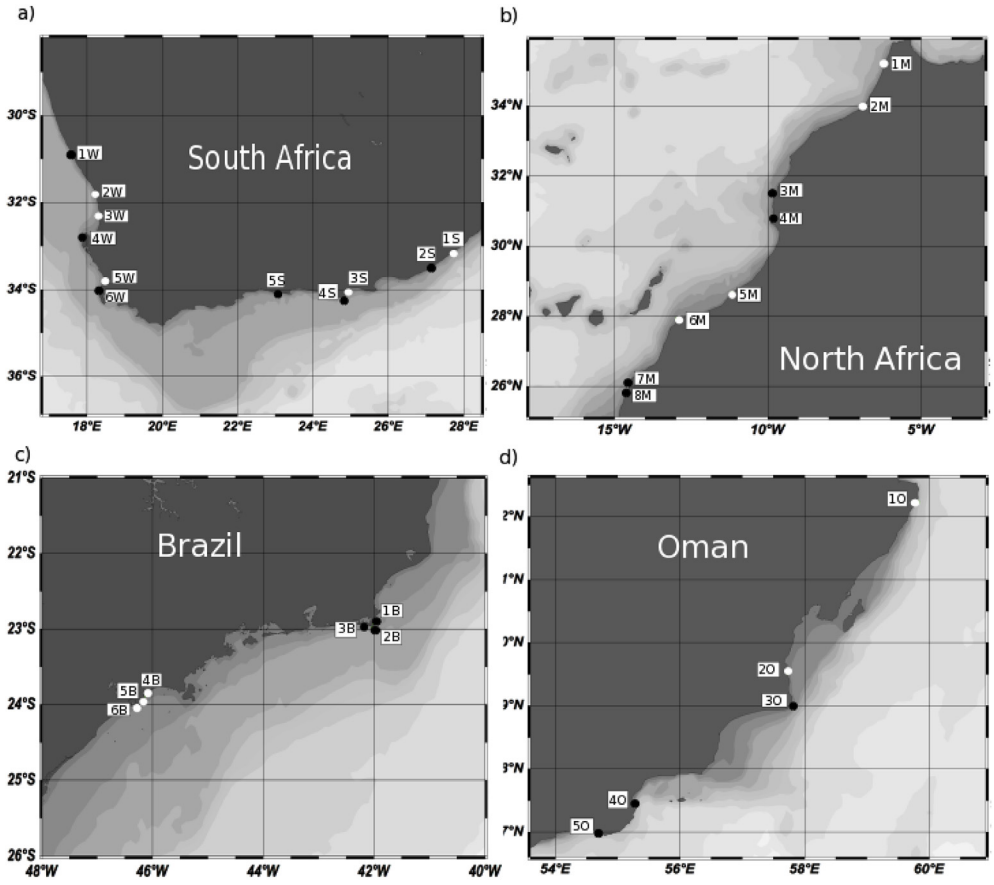

Fig. 2. Maps of the five upwelling regions investigated in the present study a) South African south and west coast, b) North West Africa, c) Brazil, d) Oman. Black symbols indicate upwelling sites while white symbols non-upwelling centres.

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Oman (Table 1; Fig. 2).

2.2.1. South Africa

Samples from South Africa were collected from recognised upwelling and non-upwelling areas on each of the south and west coasts (Fig. 2). On the west coast, samples were collected at three upwelling sites (Groenrivier, 1W; Paternoster, 4W; Llandudno, 6W) and three non-upwelling areas (Doring Bay, 2W; Elandsbaai, 3W; Bloubergstrand, 5W). Sites 2W, 3W, 5W and 6W were sampled in 2012, while 1W, 2W, 3W and 4W were sampled in 2013. Llandudno (6W) and Paternoster (4W) experience seasonal upwelling, while Groenrivier (1W) exhibits very frequent, intense upwelling events (Andrews and Hutchings, 1980).

On the south coast, samples were collected from three upwelling sites (Port Alfred, 2S; Cape St Francis, 4S; Knysna, 5S) and two non-upwelling sites (Kidd's beach, 1S; Jeffreys Bay, 3S). Sites 1S, 2S, 3S and 5S were sampled in 2012, while 1S, 2S, 3S and 4S were sampled in 2013. Port Alfred (1S) is located in the proximity of a permanent upwelling cell, while Cape St Francis (4S) and Knysna (5S) experience sporadic upwelling events throughout the year (Lutjeharms et al., 2000).

Sites 1S, 2S, 3S, 2W and 3W were sampled in both 2012 and 2013.

2.2.2. North West Africa

Samples from North West Africa were collected in 2013 at four upwelling sites (Essaouira, 3M; Imsouane, 4M; Boujdour, 7M; Qued Kraa, 8M) and four non-upwelling sites (Lorache, 1M; Rabat, 2M; Tan Tan, 5M; Tarfaya, 6M; Fig. 2). Essaouira (3M) and Imsouane (4M) are typified by very frequent upwelling events throughout the year, while Boujdour (7M) and Qued Kraa (8M) are exposed to weaker upwelling events than at other sites along the same coast (Hagen et al., 1996).

2.2.3. Oman

In Oman, samples were collected at two sites in 2014 and at three other sites in 2016. In 2014 samples were collected from an upwelling site (Mirbat, 5O) and a non-upwelling site (Al Khabbah, 1O); while in 2016 the sampling was conducted at two upwelling (Ras Madrakan, 3O; Hasik, 4O) and one non-upwelling site (Duqm, 2O; Fig. 2).

2.2.4. Brazil

On the Brazilian coast, samples were collected in 2015 from three upwelling sites (Prainha, 1B; Atalaia, 2B; Ponta da Cabeca, 3B) and three non-upwelling areas (Sao Pedro, 4B; Praia Branca, 5B; Praia Preta, 6B; Fig. 2).

2.3. Sample collection

Each of our study regions supports populations of one or both of the intertidal mussels *P. perna* and *M. galloprovincialis*. The two co-occur in North West Africa and on the south coast of South Africa. Brazil and Oman support only *P. perna* and the west coast of South Africa only *M. galloprovincialis*. Both species were collected in North West Africa, with only one species from each of the other regions. Previous comparisons showed no difference in the isotopic composition of the two species when collected from the same mussel bed (Puccinelli et al., 2017). At each site, five replicates of each target species within the same size range (approximately 5 cm) were haphazardly collected for samples of gonad (G), gill lamellae (L) and adductor muscle (M). Stable isotope turnover rates differ among tissues and are approximately nine months for adductor muscle and three months for gill tissue, while the turnover rate of gonad depends on the reproductive state of the animal (Hill et al., 2006; Hill and McQuaid, 2009). Specimens were immediately dissected and the tissues were rinsed in milliQ water and preserved frozen with the exception of Oman (2016) and North West Africa where, for logistic reasons, they were stored in 70% ethanol until returned to the laboratory.

In order to evaluate the effect of ethanol on the SI values of mussels, we ran a test comparing mussels preserved in ethanol with mussels stored in a −20 °C freezer for 30 days (time for which samples were preserved in ethanol; n = 30 individuals per condition). The analyses indicated that mussels in ethanol had lower $\delta^{15}N$ values than conspecifics preserved in −20 °C, while $\delta^{13}C$ did not differ between samples in the two conditions (ANOVA, $p < 0.01$ and $p > 0.05$, respectively). The main analyses were restricted to comparisons within regions where the preservation method was standard for all samples (Table 1). Due to the different preservation methods used for samples collected in Oman, we analysed the samples from 2014 to 2016 separately.

Additionally, because lipid content can affect the $\delta^{13}C$ composition of animals (DeNiro and Epstein, 1978), and because some of our samples had C:N ratios > 3.5‰, indicating high lipid content (see Table S1 in supplementary material), we applied a mathematical correction to all $\delta^{13}C$ data following the equation of Post et al. (2007):

$$\delta^{13}C\text{normalized} = \delta^{13}C\text{untreated} - 3.36 + 0.99*C{:}N$$

Lastly, because both *P. perna* and *M. galloprovincialis* were collected from co-occurring mussel beds in North West Africa, intra-species comparison was conducted in this upwelling region.

2.4. Bivalve stable isotope analyses

In the laboratory, samples from each region were dried at 60 °C for 48 h. The samples were ground into a fine powder with a ball mill and 1 mg subsamples were placed into tin foil capsules. Samples were analysed for SI ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) using a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system housed at the Stable Isotope Laboratory of the Mammal Research Institute (University of Pretoria, South Africa). Results are expressed in standard unit notation as:

$$\delta X(‰) = \left(\frac{[\text{Rsample} - \text{Rstandard}]}{\text{Rstandard}} - 1\right) \times 1000$$

where X is ^{13}C or ^{15}N, R represent the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Analytical precision was < 0.15‰ for $\delta^{13}C$ and < 0.1‰ for $\delta^{15}N$. Beet sugar, ammonium sulphate and casein were used as standards, calibrated against multiple International Atomic Energy reference standards. Measurement precision for both carbon and nitrogen was ± 0.05‰. All results are referenced to Vienna Pee-Dee Belemnite for carbon isotope values, and to air for nitrogen isotope values.

2.5. Data analysis

We analysed the effects of upwelling on tissue $\delta^{13}C$ and $\delta^{15}N$ isotope compositions within each region using a mixed model design consisting of the factors: Upwelling (two levels, fixed), Site (two/three levels, random and nested in Upwelling) and Tissue (three levels, fixed and crossed with all the other factors). For South Africa, we report the results of the 2012 investigation by Puccinelli et al. (2016a), and ran the analyses for the 2013 investigation separately. Significant ANOVA effects were followed by Tukey HSD *post hoc* tests. Levene's and Shapiro Wilks tests were used to confirm homogeneity of the variances and normality, respectively. Analyses were performed using STATISTICA v12 (StatSoft Inc. 2012).

3. Results

Upwelling had significant effects in almost all analyses, but with frequent significant interactions with tissue (Table 2). Overall, there were few effects of upwelling on $\delta^{15}N$, and as expected, we detected significant effects of tissue type on $\delta^{13}C$ (gonad < gill ≤ adductor muscle) in all regions. Generally, tissue $\delta^{13}C$ values were lower at

Table 2
ANOVA results performed on the $\delta^{15}N$ and $\delta^{13}C$ of the filter feeders *Perna perna* and *Mytilus galloprovincialis* at upwelling and non-upwelling sites along the coasts of a) Oman, South Africa west and south coasts, b) North West Africa and Brazil. n = 5 per site, for each species and tissue. For South Africa samples collected in 2012 we only had adductor muscle tissue. df = degrees of freedom. MS = mean square. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

a)

Factors		South Africa west coast-2012				South Africa south coast-2012			
		df	MS	F	P	df	MS	F	p
$\delta^{13}C$	Upwelling	1	25.86	247.03	***	1	3.74	24.08	***
	Site (Upwelling)	2	11.40	108.87	***	2	4.52	29.13	***
	Error	36	0.11			36	0.11		
$\delta^{15}N$	Upwelling	1	0.04	0.25		1	3.73	21.20	***
	Site (Upwelling)	2	2.19	13.91	***	2	13.16	74.73	***
	Error	36	0.16			36	0.18		

Factors		South Africa west coast-2013				South Africa south coast-2013				Oman-2014				Oman-2016			
		df	MS	F	P	df	MS	F	p	df	MS	F	p	df	MS	F	p
$\delta^{13}C$	Upwelling	1	1.71	9.10	**	1	0.10	0.90		1	109.09	137.95	***	1	58.02	324.45	***
	Site (Upwelling)	2	15.73	83.8	***	2	9.11	80.60	***					1	50.53	282.53	***
	Tissue	2	7.22	38.50	***	2	1.23	10.90	***	2	20.16	25.50	***	2	0.33	1.85	
	Upwelling*Tissue	2	1.52	8.10	***	2	0.24	2.10		2	1.18	1.49		2	2.69	15.04	***
	Site (Upwelling)*Tissue	4	1.87	10.00	***	4	0.04	0.40						2	3.32	18.57	***
	Error	108	0.19			103	0.11			24	0.79			36	0.16		
$\delta^{15}N$	Upwelling	1	0.52	3.74		1	1.45	7.35	**	1	6.99	6.04		1	0.72	8.97	**
	Site (Upwelling)	2	6.34	45.80	***	2	16.34	82.82	***					1	4.90	61.35	***
	Tissue	2	14.27	103.05	***	2	6.51	32.99	***	2	0.06	0.09		2	3.15	39.38	***
	Upwelling*Tissue	2	0.27	1.96		2	0.31	1.59		2	1.49	2.36		2	0.08	0.95	
	Site (Upwelling)*Tissue	4	0.50	3.59		4	0.32	1.64						2	0.55	6.86	**
	Error	108	0.14			103	0.20			24	0.63			36	0.08		

b)

Factors		North West Africa-*Perna perna*				North West Africa-*Mytilus galloprovincialis*				Brazil-2015			
		df	MS	F	p	df	MS	F	p	df	MS	F	p
$\delta^{13}C$	Upwelling	1	35.18	134.80	***	1	22.82	59.19	***	1	27.62	895.7	***
	Site (Upwelling)	6	8.59	32.90	***	6	18.92	49.08	***	2	7.17	232.6	***
	Tissue	2	16.47	63.10	***	2	19.48	50.53	***	2	0.07	2.20	
	Upwelling*Tissue	2	0.07	0.30		2	0.03	0.08		4	0.31	10.00	***
	Site (Upwelling)*Tissue	12	1.31	5.00	***	11	1.71	4.43	***	8	0.12	3.80	***
	Error	93	0.26			83	0.39			72	0.03		
$\delta^{15}N$	Upwelling	1	0.65	6.12	*	1	1.08	11.95	***	1	2.14	43.68	***
	Site (Upwelling)	6	5.36	50.47	***	6	8.11	89.95	***	4	0.05	1.12	
	Tissue	2	2.04	19.16	***	2	8.51	94.36	***	2	0.59	12.01	***
	Upwelling*Tissue	2	0.50	4.75	*	2	0.07	0.75		2	0.33	6.80	**
	Site (Upwelling)*Tissue	12	0.28	2.61	**	11	0.24	2.62	**	8	0.07	1.48	
	Error	93	0.11			83	0.09			72	0.05		

upwelling sites in all regions except North West Africa where the pattern was more variable (see Table S1 in supplementary material).

3.1. South Africa west coast

Results from the first investigation in South Africa in 2012 are reported in Puccinelli et al. (2016a). Briefly, only adductor tissue was sampled and its $\delta^{13}C$ value was lower at upwelling sites than at non-upwelling sites, while $\delta^{15}N$ was not affected (Table 2). In 2013 the pattern was different (Figs. 3–5), with no effects of upwelling on $\delta^{15}N$ and fewer on $\delta^{13}C$ values. Gill samples at non-upwelling sites had $\delta^{13}C$ values (Fig. 5) that were non-significantly dissimilar from the corresponding upwelling sites (Table 2). In contrast, gonad had significantly lower $\delta^{13}C$ at upwelling sites than non-upwelling areas (Fig. 4), while only adductor muscle tissue from site 3W had a lower $\delta^{13}C$ (-15.20 ± 0.15‰; Fig. 3) compared to the corresponding non-upwelling site (-14.47 ± 0.25‰; Tukey HSD, $p < 0.01$). In general, gonad had the lowest $\delta^{15}N$ values among tissues (Tukey HSD, $p < 0.01$), followed by gill and adductor muscle, which did not differ.

3.2. South Africa south coast

Upwelling did not influence either the $\delta^{15}N$ or $\delta^{13}C$ compositions of mussel species and this was true for all three tissues (Table 2). There was variability between sites within the same upwelling condition but this did not change the general pattern in relation to upwelling (Figs. 3–5). Generally, gonad had the lowest $\delta^{13}C$ and $\delta^{15}N$ values among tissues (Tukey HSD, $p < 0.05$), followed by gill and adductor muscle, which did not differ (Tukey HSD, $p > 0.05$).

3.3. North West Africa

Both *P. perna* and *M. galloprovincialis* showed significant effects of the factors Upwelling, Site (Upwelling), Tissue and their interactions for both $\delta^{15}N$ and $\delta^{13}C$ (Table 2). Post hoc tests showed that sites within the same condition of upwelling or non-upwelling had different $\delta^{15}N$ and/or $\delta^{13}C$ compositions, however we could not identify a clear pattern of variation (Figs. 3–5). Generally, in both species gill had the highest $\delta^{15}N$ values followed by gonad and adductor muscle, which did not differ (Tukey HSD $p > 0.05$). Gonad of *M. galloprovincialis* had the lowest $\delta^{13}C$ (Tukey HSD, $p < 0.01$), followed by gill and adductor

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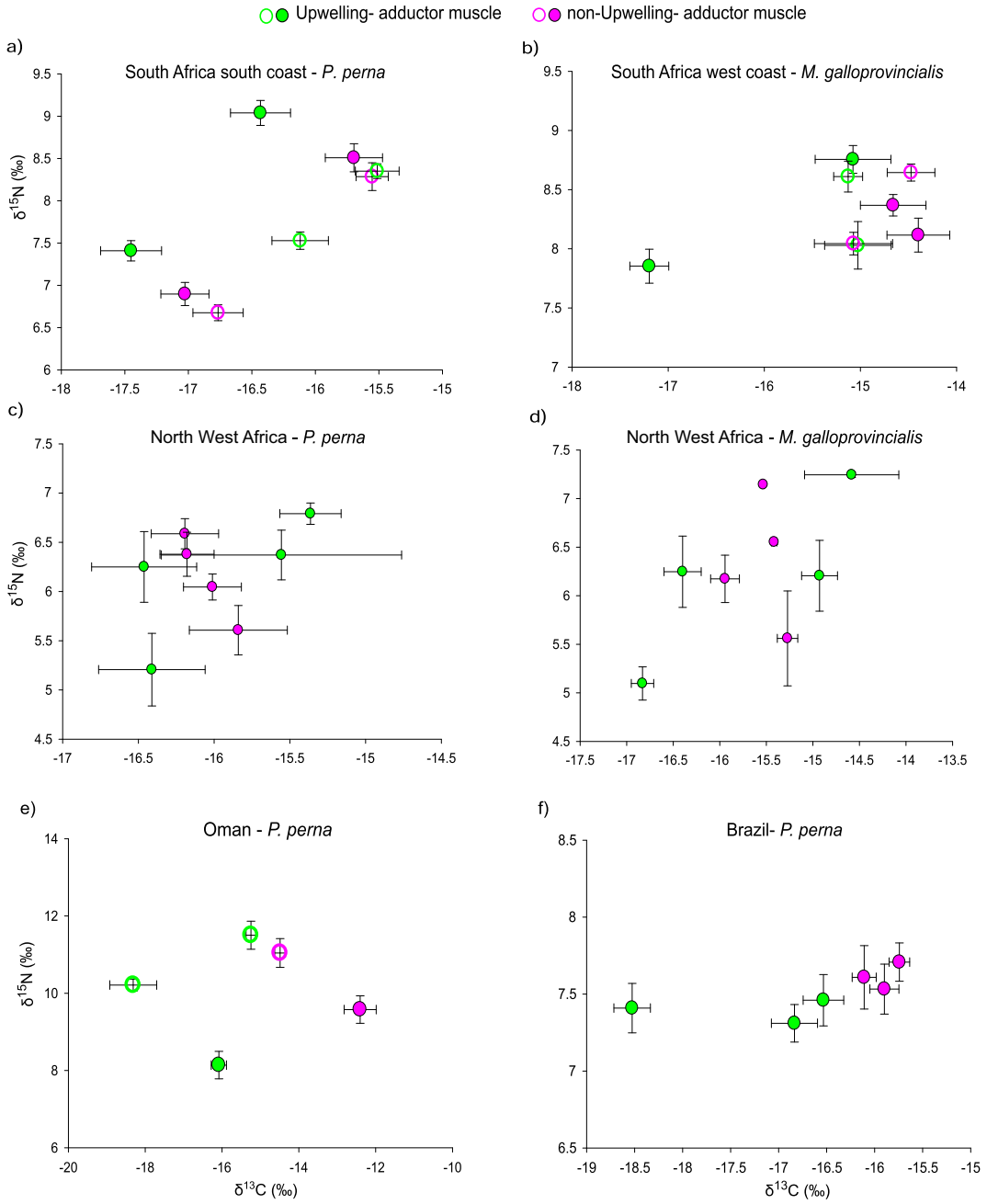

Fig. 3. Stable isotope results (mean ± standard deviation) from adductor muscle samples of *Perna perna* and *Mytilus galloprovincialis* at upwelling (green) and non-upwelling sites (pink) from the intertidal rocky shore of a) South Africa south coast b) South Africa west coast, c-d) North West Africa, e) Oman and f) Brazil. Each symbol represents the average of five replicates. In a) and b) unfilled symbols indicate samples collected in 2013 and filled symbols samples of 2012. In e) unfilled symbols indicate samples from 2014 and the filled symbols of 2016. Note that different scales were used among panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

muscle (Figs. 3 and 5), while *P. perna* showed minimal variation among tissues (Table S1 in supplementary material).

Analyses conducted to investigate possible differences between the two species, indicated that they did not differ in their $\delta^{15}N$ composition (MS = 0.068, F = 0.69, p = 0.40), while there was a significant difference in the $\delta^{13}C$ of gonad, but only at sites 3M and 4M.

3.4. Oman

$\delta^{15}N$ values from 2014 were not significantly affected by any factor, while those for specimens from 2016 were influenced by the factors Upwelling, Site (Upwelling) and Tissue (Table 2). In the latter case, $\delta^{15}N$ values varied but with no clear pattern (Figs. 3–5). $\delta^{13}C$ values of all three tissues were significantly lower at upwelling sites (mean −16.16 ± 1.69‰) than non-upwelling sites (mean -12.81 ± 1.74‰) during both surveys (Table 2; Figs. 3–5).

3.5. Brazil

For $\delta^{15}N$, only gonad showed an effect of upwelling, with non-upwelling sites having a higher $\delta^{15}N$ compared to upwelling sites. All three tissues had a lower $\delta^{13}C$ at upwelling sites (mean −17.18 ± 0.78‰) compared to non-upwelling sites (mean −16.09 ± 0.28 ‰; Figs. 3–5). Gonad generally had the lowest $\delta^{13}C$

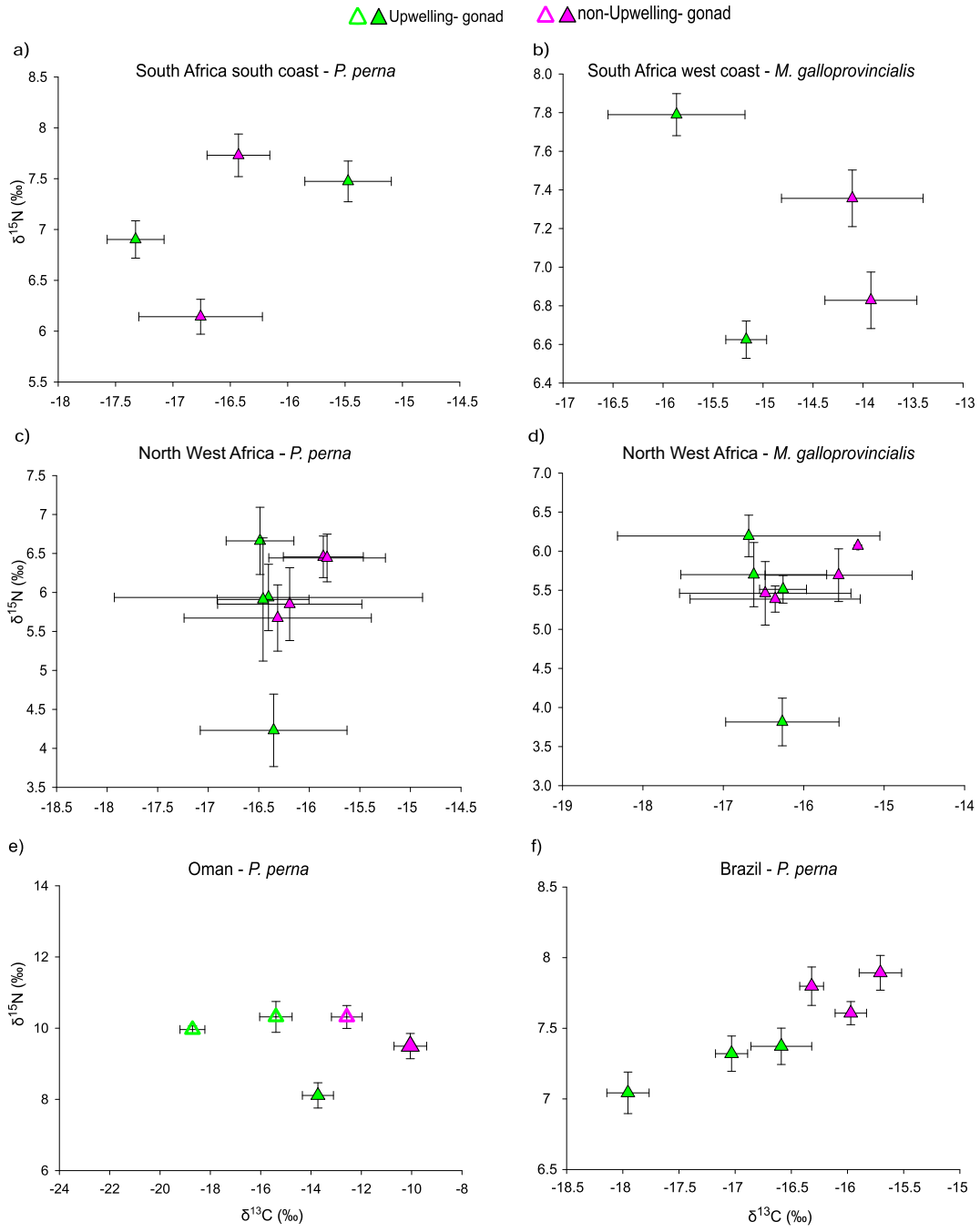

Fig. 4. Stable isotope results (mean ± standard deviation) from gonad samples of *Perna perna* and *Mytilus galloprovincialis* at upwelling (green) and non-upwelling sites (pink) from the intertidal rocky shore of a) South Africa south coast b) South Africa west coast, c-d) North West Africa, e) Oman and f) Brazil. Each symbol represents the average of five replicates. In e) unfilled symbols indicate samples collected in 2014 and the filled symbols in 2016. Note that different scales were used among panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

values among tissues, followed by gill and adductor muscle (Tukey HSD, $p > 0.05$), while $\delta^{15}N$ values were variable.

4. Discussion

Present evidence and modelling predict global increases in upwelling intensity and frequency (Sydeman et al., 2014; Bakun et al., 2015; Wang et al., 2015). While upwelling has complex effects on larval advection and delivery to the shore (Cury and Roy, 1989; Morgan et al., 2012; Shanks and Morgan, 2018), its influence on phytoplankton productivity was broadly discernible in mussel isotopic signals. The effect of upwelling on phytoplankton production is dose dependent in that it depends on the amount of nutrients injected into the water column (Frederiksen et al., 2006), which is linked to the intensity and frequency of upwelling (Bakun, 1990). This was discernible in our results, with implications for the quantity and quality of food available to filter-feeders. As filter feeders are not only the link through which pelagic primary production enters the food web, but also in many cases ecological engineers, this has implications for ecosystem structure and functioning. $\delta^{13}C$ provides an indication of the food source assimilated by organisms (Fry, 2006), SPM being the main source for benthic filter feeders. The $\delta^{13}C$ values of SPM generally decrease from onshore to offshore, reflecting a decrease in the influence of macroalgal detritus and a shift to domination of the SPM by phytoplankton (Hill et al.,

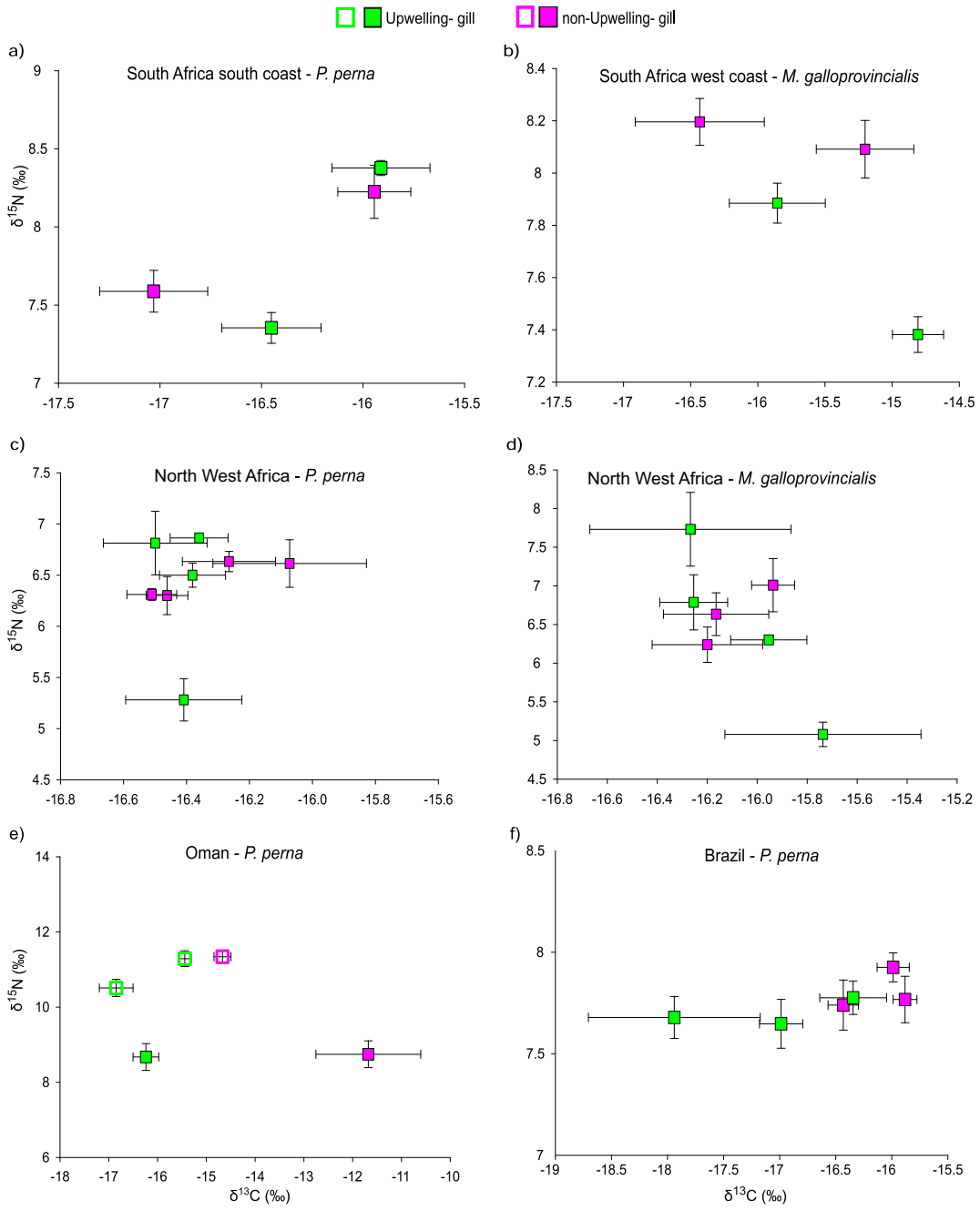

Fig. 5. Stable isotope results (mean ± standard deviation) from gill samples of *Perna perna* and *Mytilus galloprovincialis* at upwelling (green) and non-upwelling sites (pink) from the intertidal rocky shore of a) South Africa south coast b) South Africa west coast, c-d) North West Africa, e) Oman and f) Brazil. Each symbol represents the average of five replicates. In e) unfilled symbols indicate samples from 2014 and the filled symbols of 2016. Please note that different scales were used among panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2006; Mallela and Harrod, 2008). In upwelling regions, upwelled water is carried onshore during periods of downwelling and relaxation conditions (Roughan et al., 2005), or it can be retained within the area where the upwelling event takes place (Wieters, 2005). Here we tested the generality that such effects would be reflected in the diet of benthic filter feeders across several upwelling systems. Our results suggest that increased fertilisation of nearshore waters by upwelling leads to increased phytoplankton production which is then reflected in the diet of filter feeder populations.

Our results were broadly consistent across widely separated regions, with little effect of upwelling on $\delta^{15}N$, generally lower $\delta^{13}C$ values at upwelling sites and dissimilarities among tissues. In most cases, gonad showed lower $\delta^{13}C$ and $\delta^{15}N$ values than the other two tissues, which had similar values. In addition, all tissues from the same region exhibited the same pattern, regardless of differences in the intensity and frequency of upwelling, despite their different metabolic properties (Paulet et al., 2006) and isotopic turnover rates (Hill and McQuaid, 2009). Importantly, the broad pattern of low $\delta^{13}C$ values at upwelling sites was superimposed on region-specific effects. Samples from Brazil and Oman conformed to our expectations, with upwelling-associated low $\delta^{13}C$ values in all three tissues, an effect confirmed across two sampling events in the case of Oman. In the case of South Africa, our expectation was only partially confirmed, while there was no clear pattern for North West Africa.

The isotopic composition of filter-feeding primary consumers acts as a proxy for the average composition of the SPM on which they feed. In

coastal marine environments there is a clear shift in the SI composition of SPM from relatively high values ($\delta^{13}C \approx -15‰$) close to shore where SPM is dominated by macroalgal detritus and terrestrial input (France, 1995; Bustamante and Branch, 1996; Harmelin-Vivien et al., 2008), to much lower values ($\delta^{13}C \approx -22‰$) farther offshore, where SPM comprises mostly phytoplankton (Hill et al., 2006; Corbisier et al., 2014). $\delta^{13}C$ varies as a functions of several other factors (Magozzi et al., 2017), including the concentration of dissolved CO_2 (e.g. Rau et al., 1992), phytoplankton cell size, growth rate and community composition (Fry and Wainright, 1991; Popp et al., 1998), and potential terrestrial input (e.g. France, 1995). For instance, picoplankton (0.2–2 μm) usually has a lower $\delta^{13}C$ than nanoplankton (2–20 μm), and microplankton (20–200 μm) due to lower levels of isotopic fractionation than in large phytoplankton cells (Rau et al., 1990; Soares et al., 2015). Therefore, different phytoplankton communities can lead to differences in SPM $\delta^{13}C$, and consequent effects on primary consumer $\delta^{13}C$ values. Several studies have highlighted the limitations of using SPM as a baseline in trophic food web studies (McClelland et al., 2003), as it represents a snapshot of what is in the water at the moment of the sampling and does not necessarily represent average conditions (Puccinelli et al., 2018). Consequently, the timing of SPM sampling can be extremely important. For instance, different phytoplankton communities may be observed depending whether sampling is conducted before or after an upwelling event (Iriarte and González, 2004). In this study, however, we investigated the isotopic composition of primary consumers which have been shown to integrate an isotopic signal over relatively long periods (Hill and McQuaid, 2009).

$\delta^{15}N$ ratios have been considered a better indicator of upwelling conditions because newly upwelled $\delta^{15}N$ has a higher $\delta^{15}N$ value than recycled nitrogen or nitrogen fixed by diazotrophs (Miyake and Wada, 1967). Differences in the isotope composition of the nitrogen sources for primary producers would then be propagated within the food web and reflected in the $\delta^{15}N$ of primary consumers (McClelland et al., 2003). This was not, however, the case in our study. In all the regions investigated, $\delta^{15}N$ of the consumers was either not affected by upwelling or showed only small variation. This contrasts with previous studies which found an influence of upwelling on the $\delta^{15}N$ of primary producers and consumers (Viana and Bode, 2013; Vokhshoori and McCarthy, 2014). Coastal areas are, however, variable environments subject to the influence of terrestrial and anthropogenic inputs that can increase the $\delta^{15}N$ composition of primary consumers (McClelland et al., 1997; Puccinelli et al., 2016b), making it difficult to separate effects related to upwelling from those of other variables.

The low $\delta^{13}C$ values observed for filter-feeders at upwelling sites indicate a greater dependence on phytoplankton blooms generated by upwelling (Puccinelli et al., 2016a). The observed regional effects largely reflected differences in the intensity and frequency of upwelling, providing additional insights into understanding the consequences of increased upwelling. The fact that samples from Brazil and Oman conformed to our predictions reflects the persistent influence of upwelling in the areas sampled. Phytoplankton production in the Brazilian upwelling region can be five times higher than outside the upwelling system (Gonzalez-Rodriguez et al., 1992; Guenther et al., 2008), and the pivotal role of upwelling along the coast of Brazil has previously been shown for other marine components. For example, the high primary productivity associated with upwelling events increases the microbial biomass and labile organic matter content of sediments (Sumida et al., 2005), while demersal populations receive organic matter from vertical sedimentation following upwelling events (Corbisier et al., 2014). Likewise, although strongly seasonal (Yi et al., 2018), upwelling off Oman is intense (Currie, 1992; Piontkovski and Al-Jufaili, 2013) and result in massive algal blooms (Piontkovski et al., 2017). At upwelling sites, clearly lower $\delta^{13}C$ values in mussel tissues were found, even when samples were collected in two different years.

On the South African west coast, the data for 2013 only partially supported the results of the investigation conducted in 2012, with low $\delta^{13}C$ values at only one upwelling site. The discrepancy between the two years can be attributed to the spatial scales of the investigations and to variability among sites. The sites sampled in 2012 spanned 400 km of coast, including a site close to the permanent upwelling cell around Luderitz in Namibia, and the other upwelling sites sampled experience frequent, intense upwelling events (Shannon and Nelson, 1996). In contrast, the 2013 study focused on the Southern Benguela System, covering 200 km of the coast where upwelling occurs only in summer. We attribute the difference between the two sets of data to known differences in the intensity and frequency of upwelling at the sampled sites as upwelling intensity is positively correlated with nutrient availability and thus phytoplankton production (Steinacher et al., 2010). This explanation also helps explain the result for the South African south coast from 2013, which did not show an influence of upwelling. This coast is dominated by the oligotrophic Agulhas Current and upwelling events are markedly less frequent and less intense than on the west coast (Schumann et al., 1982).

North West Africa exhibited no discernible pattern due to high variability amongst sites. For both species of mussel investigated, $\delta^{13}C$ and $\delta^{15}N$ differed among sites, with no clear effect of upwelling. The coast of North West Africa is particularly productive, being classified as one of the four Eastern Boundary Upwelling Systems (EBUS; Chavez and Messié, 2009). In addition to upwelling, however, this coast experiences the influence of Saharan Desert which has been proposed as a mineral source that fertilizes the Atlantic Ocean by pushing dust westward from the desert to the Ocean (Pabortsava et al., 2017). This dust contains high concentrations of iron and phosphate, which are fundamental to phytoplankton production and frequently limit its growth (Jickells et al., 2005). The effects of such dust can be perceived as far away as the Amazon Forest (Koren et al., 2006), the Andean Forest (Fabian et al., 2009) and the West Florida shelf (Lenes et al., 2001), where Saharan dust has been identified as one of the main mineral sources regulating the productivity of these ecosystems. The results of our study suggest that the North West African coast receives nutrients from both upwelling and Saharan dust. This, combined with low offshore phytoplankton advection due to alongshore coastal circulation in this region (Auger et al., 2016), will have the effect of promoting phytoplankton growth at non-upwelling sites as well as upwelling sites, leading to either similar $\delta^{13}C$ values or to variability among sites that cannot be attributed solely to the influence of either upwelling or Saharan dust. This resulted in the impossibility of separating the effects of upwelling from those of Saharan dust with the methodology used and current information available. The North West Africa region also showed significant effects of upwelling on mussel $\delta^{15}N$ compositions, however without a clear pattern of variation. These effects can also be related to the Saharan input. Saharan fertilisation has been shown to be linked to increased atmospheric N_2-fixation, a process that leads to lower $\delta^{15}N$ values in the nitrogen source (Sigman et al., 2001; Montoya et al., 2002) and to a different phytoplankton community composition from those of an upwelling system (Fernández et al., 2013; Ratten et al., 2015). This depletion in $\delta^{15}N$ is propagated through the food web (McClelland et al., 2003), leading to a pattern in $\delta^{15}N$ that is opposite to the expected increase in $\delta^{15}N$ associated with upwelling and helping to generate the variability observed in the $\delta^{15}N$ values of mussels in North West Africa.

In addition to addressing our primary question, the results provide insight into two other aspects. First, the two mussel species were collected from the same beds in North West Africa providing an opportunity to investigate species-specific effects. Although they may differ in their metabolism or feeding mechanisms (Puccinelli et al., 2017), the two species showed no significant dissimilarities in their SI composition, again providing insight into generality. Second, we analysed the effects of tissue type. Of the three tissues investigated, gonad has the fastest turnover rate, though this is linked to the time of spawning which can differ markedly among species (Porri et al., 2006). Despite the different isotope turnover rates of the tissues, which ranged

between approximately nine and three months for adductor muscle and gill respectively (Hill and McQuaid, 2009), the three tissues responded similarly to the effects of upwelling, suggesting that a similar signal is integrated over short and long-term periods. In addition, our data allowed us to test the effects of mathematical delipidation. Lipid content can have an observable effect on the $\delta^{13}C$ composition of marine specimens when the C:N ratio is higher than 3.5 (Post, 2007). In our case, we had samples with ratios of up to 10.24 in Oman. This was particularly the case for gonads, which can store a large amount of lipids for sperm and egg production (Duinker et al., 2008). We found that mathematically correcting for high lipid content did alter some results, but not in such a way as to affect the overall patterns seen.

Our study highlights the pivotal influence that upwelling has on food availability for coastal benthic filter feeders, but with variability among systems, indicating that the effects of upwelling are nested within system-specific factors. Saharan dust for instance, influenced the North West Africa upwelling system; similarly, the intensity and frequency of upwelling events as well as the current regimes characteristic of each region (e.g. Benguela vs Agulhas Current in South Africa), were important drivers of SI variation. Essentially the effects of upwelling are dose-dependent with stronger consequences for consumer diets where upwelling is more intense and/or frequent, though this can be masked by alternative sources of phytoplankton fertilisation, as in North West Africa.

These results have important implications for understanding the consequences of the effects of climate change on upwelling events. An increase in upper-ocean temperature is expected, as a result of global warming (Levitus et al., 2000). This will promote vertical stratification, which can result in nutrient depletion in the euphotic zone and decreased phytoplankton production at middle and low latitudes (Behrenfeld et al., 2006). This, in turn, favours an increase in small picoplankton, and less efficient energy transfer through planktonic food webs with the consequence of reducing energy flow to higher trophic levels (Morán et al., 2010). Such effects can directly influence trophic dynamics in coastal areas by decreasing the amount and quality of food available for primary producers and consumers (Hallegraeff, 2010), with cascading effects on the functioning of the entire ecosystem. However, climate change is also expected to increase upwelling frequency and intensity due to a poleward shift of the high-pressure cells that affect wind patterns (Sydeman et al., 2014). This will lead to increased nutrient supply in upwelling areas, highlighting the contrast with non-upwelling influenced sites, with implications for nitrogen uptake, carbon sequestration and energy transfer to higher trophic levels (Longhurst and Glen Harrison, 1989). Concomitantly, modelling studies suggested that variability in patterns of wind distribution, will also lead to a shift in the core of upwelling centres (Rykaczewski et al., 2015) and the locations of the water masses that feed upwelling cells (Song et al., 2011). This suggests that under a climate change scenario, upwelling systems may be of increasing importance as hotspots of food supply and energy transfer to coastal ecosystems and higher trophic levels (Frederiksen et al., 2006), including local and commercial fisheries (Ward et al., 2006; Bakun et al., 2015). However, at the same time, filter feeder larval supplies to coastal areas are expected to decrease if upwelling and offshore transport intensify (Iles et al., 2012). This suggests that predictions on the effects of changes in upwelling intensity and frequency on the marine food web are likely to be complex due to non-linear responses of the food-web to increased nutrient concentrations and trophic interactions (Xiu et al., 2018), combined with non-trophic effects on larval dispersal and delivery. Our results highlight the degree to which benthic coastal ecosystems are fueled by upwelling-driven primary production, while emphasizing the context-dependence of regional effects.

Authors declaration

EP, CMcD conceived the ideas and designed methodology; CMcD acquisition of funding and provision of facilities; EP, CMcD, SD and RC collected the data; EP analysed the data; EP, CMcD interpretation of data; EP led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval.

Conflicts of interest

The authors declare that no competing interests are present. Declarators of interest: none.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2019.03.015.

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